

TAXONOMIC STATUS OF THE AUSTRALIAN MAYFLY GENERA *JAPPA* AND *ULMEROPHLEBIA* (EPHEMEROPTERA: LEPTOPHLEBIIDAE)¹

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ABSTRACT: The Australian burrowing mayfly genera *Jappa* and *Ulmerophlebia* are confirmed as monophyletic groups. Their adult and larval stages are redescribed and their egg stages are newly described. Additional taxonomic and phylogenetic discussions are provided.

KEY WORDS: Ephemeroptera, Letophlebiidae, *Jappa*, *Ulmerophlebia*, Australia.

The Australian mayfly genera *Jappa* Harker and *Ulmerophlebia* Demoulin (Leptophlebiidae) are unique among Ephemeroptera because of the convergent adaptation with the burrowing mayflies (Ephemerioidea) from the Northern Hemisphere (Campbell, 1990; Bae and McCafferty, 1991, 1995). Members of the Ephemerioidea do not occur in Australia, and these are the genera of Ephemeroptera most closely adapted to hyporheic habitats in Australia. The larvae are generally found under cobble- or boulder-sized stones embedded in sand and silt substrate in mid-sized to large lowland streams (Riek, 1970; Peters and Campbell, 1991; Edmunds and McCafferty, 1996).

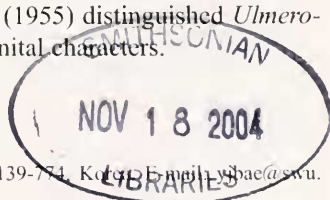
The larvae of *Jappa* possess a characteristic head with a two-pronged frontal process or "cephalic tusks" (Fig. 1) that is analogous to the mandibular tusks of Ephemerioidea, in particular those of Potamanthidae (see Bae and McCafferty, 1991: Figs. 11-14), while the larvae of *Ulmerophlebia* lack such structure (Fig. 2). Despite this morphological difference, the generic distinction of the genera has been continuously questioned by mayfly taxonomists not only because their general morphology in adult and larval stages is similar, but because generic concepts have not been well defined.

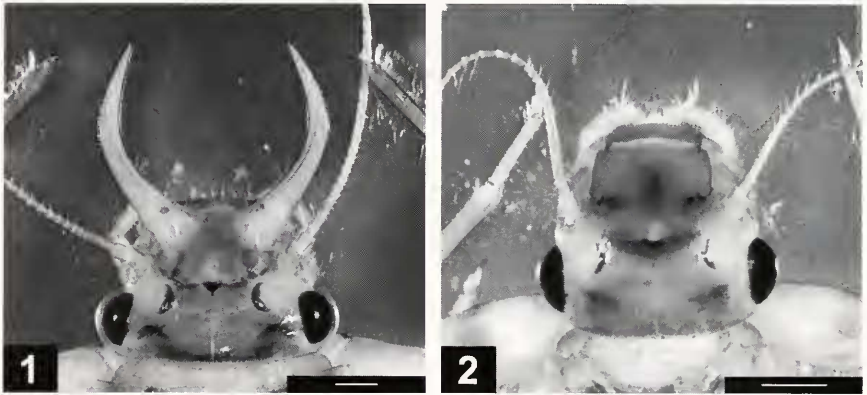
Harker (1954) established the genus *Jappa* based on adult and larval stages. At that time, forewing length to width ratio and "a burrowing type larva" with tusk-like head frontal processes or "horns" were used as the major defining characteristics. Demoulin (1955) erected the genus *Ulmerophlebia* to include a species, *Euphyurus mjobergi* Ulmer, described (as an adult only) by Ulmer (1916), but did not compare it with *Jappa*. Previously, Ulmer (1920) recombined *E. mjobergi* with *Deleatidium* Eaton; and Demoulin (1955) distinguished *Ulmerophlebia* from *Deleatidium* mainly by wing and genital characters.

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Figs. 1-2. Larval head: 1. *Jappa kutera* (bar = 0.5mm). 2. *Ulmerophlebia mjobergi* (bar = 0.5mm).

Williams (1968) mentioned a possible congeneric status of *Jappa* and *Ulmerophlebia* based on personal communication with E. F. Riek. Riek (1970), in the Ephemeroptera chapter of the textbook "The Insects of Australia," placed all burrowing Australian leptophlebiids, i.e. *Jappa* and *Ulmerophlebia*, into *Jappa* without any explanations. Peters and Campbell (1991) also followed the previous classification by Riek (1970) in the second edition of the textbook. Suter (1986) provided a historical background of *Ulmerophlebia* and described the larval stage of *Ulmerophlebia* for the first time based on a second species, *U. pipinna* Suter, but was conservative in clarifying the generic status of the *Ulmerophlebia* and *Jappa*. Dean (1999) gave larval diagnoses of *Jappa* and *Ulmerophlebia* when he provided larval keys to three nominal and four unnamed species of *Jappa* and four unnamed species of *Ulmerophlebia*, but still did not resolve the generic status.

For the above reasons, the generic concepts of *Jappa* and *Ulmerophlebia* have not been fully resolved. The purpose of this study is to clarify and delineate the genera and provide detailed redescrptions of adult, larval, and egg stages.

Type and voucher specimens and additional fresh materials of all previously known species of *Jappa* and *Ulmerophlebia* (see Species included, pp. 5, 7) are housed mainly in the Museum of Victoria, Australian National Insect Collection in Canberra, and Monash University and were examined for this study. Terminology, measurement, and other general methods are after Bae and McCafferty (1991).

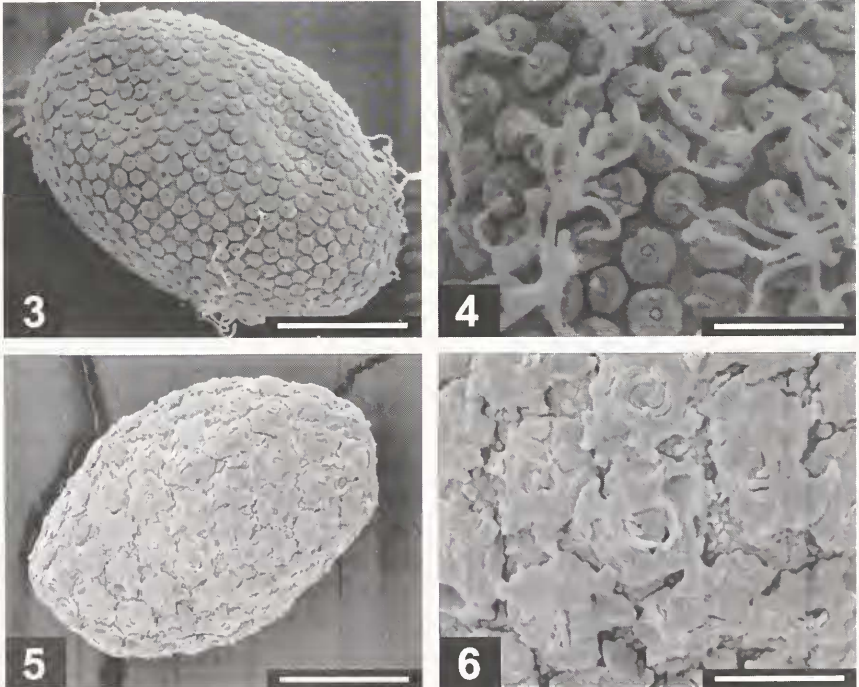
Jappa Harker

Jappa Harker, 1954: 257 [Type species: *Jappa kutera* Harker, by original designation; M & L]; Williams, 1968: 170 (L key); Dean and Suter, 1996: 44 (L); Dean, 1999: 34 (L).

Adult. Male body length 9.4-11.3 mm; female body 12.0-16.5 mm; caudal filaments 14.0-19.1 mm. General body color light yellow with dark purplish brown markings. **Head:** Male dorsal compound eyes 1.10-1.43 mm in length, 1.00-1.19 mm in width, 0.48-0.68 mm in height, broadly meeting posteromedially ($B/D = 0$), dome-shaped, dorsally oval, and with anterior margin round and posterior margin somewhat attenuating from lateral view ("bicycle helmet" shaped); basal compound eyes anteroventrally pronounced, invisible to slightly visible from dorsal view, 0.67-0.87 mm in length, 0.43-0.58 mm in height, and anteriorly oriented from lateral view. Female compound eyes 0.33-0.47 mm in width and 1.53- 1.67 mm in distance between compound eyes ($B/D = 3.50-4.70$). **Thorax:** Forewings transparent, often with dark purplish brown markings at basal, central, and apical areas, 8.8-15.6 mm in length, and 2.9-5.3 mm in width; longitudinal veins light brown to dark purplish brown; crossveins light brown to dark purplish brown (basally and anteriorly located crossveins often darker and more heavily infuscated); crossveins C-Sc 20-30, Sc-R1 16-20, and R1-R2 13-15 in number; crossveins in stigmatic area not anastomosed; MP2 basally connected to MP1 and CuA; ICu1 basally connected to CuA and CuP (angle between ICu1 and crossvein ICu1-CuP larger than angle between ICu1 and crossvein ICu1-CuA). Hindwings transparent, 2.3-2.9 mm in length, and 1.2-1.4 mm in width; longitudinal veins white to light yellow; crossveins C-Sc, Sc-R1, and some in distal part sometimes dark brown; Sc ending relatively distally (length of Sc / distance from base of Sc to apex of distal margin = 0.89); crossveins C-Sc 9-11, more or less evenly distributed (in one species, C-Sc crossveins apically concentrated); costal margin round, with weakly developed costal projection at midlength; Rs 0.48-0.68 mm; R1 0.64-0.98 mm; MPs 0.25-0.48 mm; MP1 1.11-1.37 mm. Male forefemora 2.10-2.27 mm, foretibiae 2.90-3.25 mm, foretarsal segments 1, 2, 3, 4, and 5 0.13-0.14 mm, 1.08-1.27 mm, 1.00-1.18 mm, 0.76-0.89 mm, and 0.38-0.44 mm (foretarsal segment 2 > 3 > 4 > 5 > 1), and foreclaws 0.15-0.24 mm. Female foretibiae > forefemora > foretarsi. Claws dissimilar. **Abdomen:** Abdominal segment 9 with moderately to well developed posterolateral projections. Penes Y-shaped or V-shaped, relatively long (height of penis / height of forceps segment 1 = 0.45-0.56); forceps 3-segmented, with segment 1 0.92-1.03 mm, segment 2 0.10-0.13 mm, and segment 3 0.08-0.12 mm in length; forceps segment 1 basally broad and apically slender, with relatively abrupt constriction (constriction angle 80-110°) at mid-length to 3/4 apically; forceps segments 2 and 3 often indistinctly demarcated. Caudal filaments light yellow, often with purplish brown to dark brown stripes, often with maculation at joints; cerci 1.3-1.7x length of body; terminal filament as long as cerci.

Larva. Male body length 10.4-16.9 mm; cephalic tusks 1.0-2.0 mm; caudal filaments 5.9-10.9 mm. Female body length 10.4-23.8 mm; cephalic tusks 1.4-3.5 mm; caudal filaments 5.9-18.1 mm. Body surface glassy and heavily setose. General body color light yellow to light brown with dark purplish brown markings. **Head:** Head (Fig. 1) 1.30-2.38 mm in length and 1.75-4.13 mm in width. Male compound eyes dorsally 0.56-0.60 mm in width and 0.65-1.06 mm in distance between compound eyes ($B/D = 1.08-1.76$). Female compound eyes dorsally 0.23-0.56 mm in width and 1.38-2.86 mm in distance between compound eyes ($B/D = 4.75-6.11$). Antennae 4.4-6.3 mm in length, with whorls of hairlike setae at each segment. Cephalic tusks arched and attenuating, apically convergent and upward, 1.32-2.30 mm in inner length and 1.58-2.88 mm in outer length, 14.9-26.5° in curvature; each cephalic tusk with rudimentary to distinct dorsal ridge, with small to large basodorsal tubercle, with fields of 6-20, 5-15, and 10-20 hairlike setae at basomedial, basosublateral, and apicodorsal areas (in two species apicodorsal setal field lacking), respectively, sometimes with lateral row of 1-4 spines (in one species lateral spine single and prominent), and sometimes with additional dorsolateral row of 6-13 spines. Labrum distally wider (maximum length 0.30-0.38 mm; basal width 0.59-0.87 mm; distal maximum width 0.75-1.06 mm); dorsal surface heavily setose, with basal and subapical hairlike setal fringes (basal setae longer than subapical setae); subapical setal fringe laterally longer and 8-15 setae densely arranged medially; anterior and lateral margins with hairlike setal row; anterior margin concave, with prominent median tubercle, and with three pairs of rudimentary submedian denticles; ventral surface with dense hairlike setal field along anterior margin, with row of 10-20 stout setae on subanterior margins, and with fields of 20-50 hairlike setae at submedian areas.

Mandible dorsolateral margins with very long hairlike setal row; ventral surface with transverse row of 10-20 hairlike setae; inner incisors slightly smaller to as large as outer incisors; incisors with 2-3 apical teeth and 0-4 lateral denticles; prostheca rudimentary, with well-developed fringe. Hypopharynx superlinguae laterally curved and apically pointed. Maxillae with dense hairlike setal field medially 3/4 on galealacinial crown, mixed with rowed comblike setae medially 1/2 on galealacinial crown, with one pronounced comblike seta medioapically, and with rowed dense hairlike setae on medial margin; maxillary palp segment 1 0.27-0.52 mm, segment 2 0.37-0.48 mm, and segment 3 0.19-0.37 mm in length; segment 1 and 2 with sparse hairlike setae along outer margin; segment 3 indistinctly demarcated from segment 2, with pronounced outer margin, and with strongly developed setal field along outer margin. Labial glossae dorsoventrally elongated and ventrally stalked, with dense hairlike setae; paraglossae with dense hairlike setal field dorsoapically; labial palp segment 1 0.28-0.59 mm, segment 2 0.31-0.40 mm, and segment 3 0.22-0.32 mm in length; segment 3 indistinctly demarcated from segment 2, apically pointed, with dense hairlike setal field along outer margin, and with stout setal row along inner margin. *Thorax*: Pronotum anterolateral margins round; lateral margins with row of sparse to dense hairlike setae. Forefemora 1.67-4.88 mm, foretibiae 1.67-5.63 mm, foretarsi 0.71-1.63 mm, and foreclaws 0.24-0.63 mm in length (foretibiae \geq forefemora > foretarsi > foreclaws); forefemora with long hairlike setal fields along anterior and posterior margins and basomedial area on dorsal surface; foretibiae with dense hairlike setal field (filtering setae) rowed along inner and outer margins (dorsomedially bare), with stout setal field (raking setae) on 2/3 apical to entire inner margin; foretarsi with dense hairlike setae on dorsal and lateral surfaces; foreclaws apically darker, with 10-15 tiny teeth 3/4 basally. Midlegs and hindlegs heavily setose; length femora > tibiae > tarsi > claws. *Abdomen*: Terga light brown to light purplish brown, mostly with submedian and sublateral dark purplish brown stripes, with very long hairlike setae covered on 1/2-3/4 dorsal area along median line, and with hairlike setal row along lateral margins; abdominal segment 8-9 with moderately to well developed posterolateral projections. Sterna bare (sterna 9-10 sometimes with hairlike setae). Gills on abdominal segment 1-7, double; both lamellae with indistinct to distinct



Figs. 3-6. Eggs: 3. *Jappa kutera* (bar = 38 μ m), 4. *J. kutera*, in part (bar = 10 μ m), 5. *Ulmerophlebia mjobergi* (bar = 43 μ m), 6. *U. mjobergi*, in part (bar = 17.6 μ m).

tracheae, with single apical filament; gill lamella inner part strongly expanded apicolaterally, and with fine setae on 1/5-1/2 apical margin; gill lamella outer part with fine setae on entire margin; apical filament attenuating, marginally with fine setae; gills 4 1.38-2.86 mm in length, 0.78-1.83 mm in width, and 1.38-2.38 mm in filament length, with weakly to strongly developed apical expansion. Caudal filament segments with whorls of setae.

Egg. Egg (Fig. 3) oval; long axis 124 μ m; short axis 80 μ m. Color light yellow in nature, white in alcohol. Egg surface (Fig. 4) with ca. 780 knob-terminated coiled threads relatively evenly distributed throughout egg surface; diameter of knob-terminated coiled threads 3.9-4.5 μ m. Polar caps absent. Micropyles several, scattered, tageniform; sperm guide circular, 2.6-3.3 μ m in diameter.

Diagnosis. Adults of *Jappa* possess greater numbers of C-Sc crossveins (20-30) in the forewings and more or less evenly distributed C-Sc crossveins in the hindwings (excluding one species), while those of *Ulmerophlebia* possess fewer C-Sc crossveins (12-19) in the forewings and apically concentrated C-Sc crossveins in the hindwings. The hindwing vein Sc of *Jappa* ends relatively distally (length of Sc / distance from base of Sc to apex of distal margin = 0.89) comparing with that of *Ulmerophlebia* (0.76). The penes of *Jappa* are relatively longer (height of penis / height of forceps segment 1 = 0.45-0.56) than those of *Ulmerophlebia* (0.08-0.31). The constriction in the medial margin of forceps segment 1 of *Jappa* is relatively abrupt (angle 80-110°), while that of *Ulmerophlebia* is relatively gradual (angle 135-150°). The larvae of *Jappa* can easily be distinguished from those of *Ulmerophlebia* and any other leptophlebiid genera by the cephalic tusks (Fig. 1). In addition, the body size of *Jappa* in both of the adults and larvae (adult 9.4-16.5 mm, larva 10.4-23.8 mm) is generally larger than that of *Ulmerophlebia* (adult 6.9-8.7 mm, larva 5.5-10.0 mm).

Species included. *Jappa kutera* Harker (1954), *J. edmundsi* Skedros and Polhemus (1986), *J. serrata* Skedros and Polhemus (1986), *Jappa* AV1 (Dean, 1999), *Jappa* AV2 (Dean, 1999), *Jappa* AV3 (Dean, 1999), and *Jappa* AV4 (Dean, 1999).

Distribution. NSW, NT, northern WA, QLD, and VIC.

Remarks. There are several other species previously considered as, or assigned to, *Jappa*. *Jappa tristis* Harker (1954) [Holotype stage: M; locality: Tasmania, Cradle Mt.; deposition: British Museum (Natural History)] was subsequently identified as *Tillyardophlebia* Dean by Dean (1999). *Jappa* is not considered present in Tasmania.

Leptophlebia furcifera Eaton (1871) [Type stage: M; locality: Melbourne; deposition: Melbourne Museum = Museum of Victoria], recombined with *Atalophlebia* Eaton by Eaton (1884), was considered in *Jappa* by Dean (1999). However, the type specimen was not preserved in the Museum of Victoria when YJB checked in 2001 and there is little evidence that this species belongs to *Jappa* based on Eaton's original description (Eaton, 1871) and redescription (Eaton, 1884).

Leptophlebia strigata Eaton (1871) [Type stage: F; locality: North Australia; deposition: McLachlan Collection in British Museum (Natural History)], recombined with *Atalophlebia* by Eaton (1884) and *Deleatidium* by Ulmer (1920), was also considered in *Jappa* by Dean (1999). The original description (Eaton, 1871) and redescription (Eaton, 1884) of the species do not clearly substantiate the

generic position, and it is crucial that the types be reexamined before generic placement can be confirmed.

Ulmerophlebia Demoulin

Ulmerophlebia Demoulin, 1955: 228 [Type species: *Euphyurus njobergi* Ulmer, by original designation; A]; Suter, 1986: 352 [M & L]; Dean and Suter, 1996: 44 [L]; Dean, 1999: 74 [L].

Adult. Male body length 6.9-8.7 mm; female body 6.3-8.6 mm; caudal filaments 7.5-9.5 mm. General body color light yellow with dark purplish brown markings. **Head:** Male dorsal compound eyes 0.92-0.98 mm in length, 0.78-0.87 mm in width, 0.44-0.56 mm in height, 0-0.05 mm in distance between compound eyes (B/D = 0-0.06), dome-shaped, dorsally oval, and with anterior margin round and posterior margin somewhat attenuating from lateral view ("bicycle helmet" shaped); basal compound eyes anteroventrally pronounced, invisible to slightly visible from dorsal view, 0.52-0.66 mm in length, 0.29-0.36 mm in height, and anteriorly oriented from lateral view. Female compound eyes 0.22-0.29 mm in width, and 0.83-1.03 mm in distance between compound eyes (B/D = 3.11-4.91). **Thorax:** Forewings transparent, often with dark purplish brown markings at basal, central, and apical areas, 6.6-8.5 mm in length, and 2.2-3.2 mm in width; longitudinal veins light brown to dark purplish brown; crossveins light brown to dark purplish brown (basally and anteriorly located crossveins often darker and more heavily infuscated); crossveins C-Sc 12-19, Sc-R1 12-16, and R1-R2 10-14 in number; crossveins in stigmatic area not anastomosed; MP2 basally connected to MP1 and CuA; ICu1 basally connected to CuA and CuP (angle between ICu1 and crossvein ICu1-CuP larger than angle between ICu1 and crossvein ICu1-CuA). Hindwings transparent, 1.3-1.9 mm in length, and 0.7-1.0 mm in width; longitudinal veins white to light yellow; crossveins C-Sc, Sc-R1, and some in distal part sometimes dark brown; Sc ending relatively proximally (length of Sc / distance from base of Sc to apex of distal margin = 0.76); crossveins C-Sc 4-10, apically concentrated; costal margin round, with weakly developed costal projection at 1/3 basally to midlength; Rs 0.27-0.40 mm; R1 0.56-0.75 mm; MPs 0.20-0.31 mm; MP1 0.47-1.06 mm. Male forefemora 0.45-1.67 mm, foretibiae 2.22-2.83 mm, foretarsal segments 1, 2, 3, 4, and 5 0.10-0.13 mm, 0.68-0.97 mm, 0.70-0.93 mm, 0.55-0.70 mm, and 0.25-0.30 mm (foretarsal segment 2>3>4>5>1), and foreclaws 0.13-0.15 mm. Female foretibiae> forefemora>foretarsi. Claws dissimilar. **Abdomen:** Abdominal segment 9 with moderately to well developed posterolateral projections. Penes Y-shaped or V-shaped, relatively short or rudimentary (height of penis / height of forceps segment 1 = 0.08-0.31); forceps 3-segmented, with segment 1 0.63-0.68 mm, segment 2 0.06-0.09 mm, and segment 3 0.06-0.08 mm in length; forceps segment 1 basally broad and apically slender with relatively gradual constriction (constriction angle > 135-150°) at midlength to 2/3 apically; forceps segments 2 and 3 often indistinctly demarcated. Caudal filaments light yellow, often with purplish brown to dark brown stripes, often with maculation at joints; cerci 1.1-1.7x length of body; terminal filament as long as or slightly longer than cerci.

Larva. Male body length 6.2-9.8 mm; caudal filaments 5.5-10.0 mm. Female body length 6.8-11.2 mm; caudal filaments 6.3-13.2 mm. Body surface glassy and relatively less setose. General body color light yellow to light brown with dark purplish brown markings. **Head:** Head (Fig. 2) light brown, 1.27-1.40 mm in length and 1.59-1.75 mm in width. Male compound eyes dorsally 0.48-0.58 mm in width and 0.43-0.56 mm in distance between compound eyes (B/D = 0.74-1.10). Female compound eyes dorsally 0.20-0.24 mm in width and 1.10-1.35 mm in distance between compound eyes (B/D = 4.67-6.00). Antennae 4.0 mm in length, with whorls of hairlike setae at each segment. Cephalic tusks absent. Clypeus greatly developed, 0.38-0.45 mm in length, 0.68-0.90 mm in basal width, 0.64-0.83 mm in apical width, with pronounced sublateral tubercles, and with fields of 8-10 hairlike setae subapicolaterally and 4-15 hairlike setae subbasolaterally. Labrum slightly narrower than clypeus (0.92x width of clypeus), slightly wider distally (maximum length 0.28 mm; basal width 0.56 mm; distal maximum width 0.60 mm); dorsal surface moderately setose, with basal and subapical hairlike setal fringes (basal setae as long as subapical setae); subapical setal fringe laterally longer (setae curved forward) and without dense arrangement; anterior and lateral margins with dense hairlike setal row; anterior margin slightly concave, with prominent median tubercle, and with three pairs of rudimentary submedian denticles; ventral surface with dense hairlike setal field along anterior margin, with row of 15-18 stout setae on subanterior margins, and with fields of 10-15 hairlike setae at submedian areas. Mandible dorsolateral margins with very long hairlike setal row; ventral surface without setal row; inner incisors slightly smaller to as large as outer incisors; incisors with 2-

3 apical teeth and 0-4 lateral denticles; prostheca rudimentary, with well developed fringe. Hypopharynx superlinguae laterally curved and apically pointed. Maxillae with dense hairlike setal field, mixed with row of comblike setae almost entirely on galealacinial crown, without medioapical comblike seta, and with row of dense hairlike setae on medial margin; maxillary palp segment 1 0.26 mm, segment 2 0.29 mm, and segment 3 0.12 mm in length; segment 2 with sparse hairlike setae along outer margin; segment 3 indistinctly demarcated from segment 2, with moderately developed outer margin, and with moderately developed setal field along outer margin. Labial glossae dorsoventrally elongated and ventrally stalked, with dense hairlike setae; paraglossae with dense hairlike setal field dorsoapically; labial palp segment 1 0.38 mm, segment 2 0.27 mm, and segment 3 0.20 mm in length; segment 3 indistinctly demarcated from segment 2, apically pointed, with dense hairlike setal field along outer margin, and with stout setal row along inner margin. *Thorax*: Pronotum anterolateral margins round; lateral margins with row of sparse hairlike setae. Forefemora 1.15-1.50 mm, foretibiae 1.00-1.38 mm, foretarsi 0.43-0.55 mm, and foreclaws 0.15-0.25 mm in length (forefemora \geq foretibiae $>$ foretarsi $>$ foreclaws); forefemora with a few hairlike setae on dorsal and ventral surfaces, and with hairlike setal field along posterior margin (anterior margin with few hairlike setae); foretibiae with relatively sparse hairlike setae (filtering setae) dorsally and along outer margin (inner margin with few hairlike setae), with stout setal field (raking setae) 5/6 apically on inner margin; foretarsi with relatively sparse hairlike setae on dorsal and lateral surfaces; foreclaws apically darker, with rowed tiny teeth basally. Midlegs and hindlegs moderately setose; length femora $>$ tibiae $>$ tarsi $>$ claws. *Abdomen*: Terga light yellow to light brown, mostly with broad submedian dark brown stripes, without long hairlike setal field along median line, and with hairlike setal row along lateral margins; abdominal segment 8-9 with moderately to well developed posterolateral projections. Sterna bare. Gills on abdominal segment 1-7, double; both lamellae with indistinct to distinct tracheae, with single apical filament; gill lamella inner part strongly expanded apicolaterally, and with fine setae on 1/10-1/2 apical margin; gill lamella outer part with fine setae on apically 1/10 to entire margin; apical filament attenuating, marginally with fine setae; gills 4 1.11-1.67 mm in length, 0.56-0.89 mm in width, 0.95-1.43 mm in filament length, with weakly to strongly developed apical expansion. Caudal filament segments with whorls of setae.

Egg. Egg (Fig. 5) oval; long axis 149 μ m; short axis 100 μ m. Color light yellow in nature, white in alcohol. Egg surface (Fig. 6) with ca. 116 knob-terminated coiled threads nearly evenly distributed throughout egg surface, with 0.4-2.1 μ m tiny granules throughout egg surface; diameter of knob-terminated coiled threads 8.6-10.3 μ m. Polar caps absent.

Diagnosis. The adults and larvae of *Ulmerophlebia* can be distinguished from those of *Jappa* as specified above, in the diagnosis of *Jappa*. The larvae of *Ulmerophlebia* can be distinguished from other leptophlebiid genera by the following combination of characters: possessing a prominent median tubercle anteriorly on the labrum, lacking cephalic tusks, and possessing a somewhat enlarged clypeal margin with sublateral tubercles and subapicolateral and subbasolateral hairlike setal fields.

Species included. *Ulmerophlebia njobergi* (Ulmer, 1916), *U. pipinna* Suter (1986), *Ulmerophlebia* AV2 (Dean, 1999), *Ulmerophlebia* AV3 (Dean, 1999), and *Ulmerophlebia* AV5 (Dean, 1999).

Distribution. NSW, QLD, and VIC.

Remarks. *Deleatidium annulatum* Harker (1950) [Holotype: M; locality: NSW, Point Lookout, Serpentine; deposition: Australian Museum, Sydney (destroyed)] was considered as *Ulmerophlebia* by Dean (1999), but the original description of the adult (e.g. wings) by Harker (1950) does not support placement in *Ulmerophlebia* and the description of the larva (e.g. maxillary palp) by Harker (1954) does not meet the generic concept of *Ulmerophlebia*.

Atopopus spadix Harker (1950) [Holotype: M; locality: NSW, Armidale; deposition: Australian Museum, Sydney (destroyed)] was also considered as

Ulmerophlebia by Dean (1999), but the original description of the adult (e.g. wings) by Harker (1950) does not support its placement in *Ulmerophlebia*.

DISCUSSION

In the phylogeny of the Atalophlebiinae (Leptophlebiidae), the genera *Jappa* and *Ulmerophlebia* have been hypothesized to constitute a basal clade, including *Hapsiphlebia*, *Atalophlebia*, *Atalomicria*, *Acanthophlebia*, *Aprionix*, and *Kalbaybaria* (Pescador and Peters, 1980; Towns and Peters, 1980, 1996; Campbell, 1993; Christidis, 2001). This clade, also known as the *Hapsiphlebia* lineage, was defined by the synapomorphies of lateral setae of the larval abdomen and incisor denticulation of the right mandible (Pescador and Peters, 1980).

From our comprehensive examinations of the species of *Jappa* and *Ulmerophlebia* and the species of related outgroup genera, we recognize an additional clade consisting of *Jappa* and *Ulmerophlebia*. This clade is defined by the synapomorphies of 1) a setose body, 2) gills marginally clothed with fine setae, 3) a median denticle anteriorly on the labrum, 4) submedian setal fields ventrally on the labrum, and 5) lateral spines on the larval abdomen.

Jappa and *Ulmerophlebia* are thus distinct monophyletic sister groups. *Jappa* is defined by the synapomorphies of 1) cephalic tusks, 2) a hairlike setal field ventrally on the mandible, 3) double rows of hairlike setae (filtering setae) dorsally on the tibiae, and 4) a long hairlike setal field along median abdomen. The cephalic tusks (Fig. 1) are unique in Leptophlebiidae. The cephalic tusks are arched and apically convergent and upward. They also bear basodorsal tubercles and setal fields at basomedial, subbasolateral, and apicodorsal areas. The body setation in *Jappa* is more specialized in having double rows of filtering setae on inner and outer margins of tibiae and broad setal fields on forefemora and along the median line of dorsal abdomen.

The monophyly of the *Ulmerophlebia* is supported by the synapomorphy of the unique "shovel-like" clypeal development (Fig. 2). The clypeus of *Ulmerophlebia* is flattened and somewhat elongated and possesses sublateral tubercles and hairlike setal fields in the subbasolateral and subapicolateral areas.

Although the adults of *Jappa-Ulmerophlebia* clade retain many plesiomorphic characters shared with other *Hapsiphlebia* lineage groups, the larvae are quite specialized as shown herein. The hairy body is associated with the fossorial habit of the members of *Jappa-Ulmerophlebia* clade and the cephalic tusks and shovel in *Jappa* and *Ulmerophlebia*, respectively, are evidently burrowing devices. In particular, the cephalic tusks of *Jappa* are analogous to the mandibular tusks of the Potamanthidae in Ephemeroidea, their Laurasian counterpart (Bae and McCafferty, 1991, 1995), in terms of functional morphology and burrowing behavior.

As evidenced above, the genera *Jappa* and *Ulmerophlebia* are distinct monophyletic groups that are here recognized at the generic level. Presumably, this will confirm with a strict phylogenetic classification if indeed the *Jappa*-

Ulmerophlebia clade, which is unique among Australian leptophlebiids being a burrowing mayfly group, is recognized as a distinct tribe as suggested for groupings under the subfamilies of Leptophlebiidae by Peters (1980). That classification can be adopted when the generic phylogenies of the Australian Leptophlebiidae are completed.

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